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GLYCOALKALOIDS AND RESISTANCE TO THE COLORADO POTATO BEETLE IN *SOLANUM CHACOENSE* BITTER

S.L. Sinden, L.L. Sanford[1] and S.F. Osman[2]

Abstract

Resistance of 20 F_2 *Solanum chacoense* Bitter clones to the Colorado potato beetle, *Leptinotarsa decemlineata* (Say), was measured in a field test. Levels of total glycoalkaloids (TGA) and composition of the glycoalkaloid mixtures in foliage of the clones were also determined. Clones with either commersonine or dehydrocommersonine as the major foliar glycoalkaloid were significantly more resistant (lower damage ratings, fewer larvae and adult insects) than clones with solanine and chaconine. Damage ratings were negatively correlated ($r=-0.67$, $p=0.01$) with foliar TGA levels. The results indicate that the types of glycoalkaloids present in the foliage of *S. chacoense* may be as important as the level of TGA in limiting damage and numbers of insects.

Resumen

Resistencia de 20 clones F_2 de *Solanum* chacoense Bitter, al "Colorado potato beetle". *Leptinotarsa decemlineata* (Say), se evaluó en una prueba de campo. Asimismo, se determinó niveles de glicoalcaloides totales (TGA) y composición de mezclas de glicoalcaloides en el follaje. Clones con cualquiera de los dos commersonine o dehydrocommersonine como el mayor componente de glicoalcaloide en el follaje fueron significativamente mas resistentes (lecturas bajas de daños, pocas larvas e insectos adultos) que clones con solanine y chaconine. Las lecturas de daño mostraron correlación negativa ($r=-0.67$, $p=0.01$) con los niveles de glicoalcaloides totales en el follaje (GA). Los resultados indicaron que los tipos de glicoalcaloides presentes en el follaje de *S. chacoense* puede ser tan importante como el nivel de glicoalcaloides totales en la limitación del daño y número de los insectos.

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KEY WORDS: solanine, chaconine, commersonine, leptines, *Solanum tuberosum*, *Solanum chacoense*, Colorado potato beetle, glycoalkaloids, potato.

Introduction

The resistance of certain wild *Solanum* species to the Colorado potato beetle (CPB) *Leptinotarsa decemlineata* (Say), may be due to the high levels or unusual types of glycoalkaloids found in the leaves of these species (3, 9, 14, 15). *Solanum chacoense* is one of the most resistant of the tuber-bearing *Solanum* species (8, 17). However, attempts to transfer the resistance of this wild species to a potato cultivar have not been successful. Tubers of hybrids between *S. chacoense* and *S. tuberosum* tended to have higher than normal total glycoalkaloid (TGA) contents and many of the tubers had a bitter flavor (11). Schwarze (12) found no relation between TGA contents of leaves and resistance to the CPB among these hybrid clones.

Leaves of resistant *S. chacoense* are reported to contain solanine, chaconine, leptines, and leptinines (4, 15), while most susceptible *S. tuberosum* leaves contain only solanine and chaconine (10, 13) (Fig.1). Leptine-type glycoalkaloids in *S. chacoense* leaves may be a resistance factor in this species, since leptine I is a potent CPB repellent, completely inhibiting feeding by the CPB at a concentration of 1 mM (15). In contrast, solanine (sol) and chaconine (chac) inhibited feeding only ca 50% at a concentration of 6 mM in potato leaf disks infiltrated with the individual glycoalkaloids. Tomatine (tom) and demissine (dem) were both intermediate in activity, inhibiting feeding by ca 50-70% at a concentration of 0.8 mM (15).

Although Schwarze (12) attempted to relate the resistance of certain *S. chacoense* × *tuberosum* hybrid clones that had low foliar TGA to the presence of dem or leptine I, he was unable to detect dem in any of the clones, and he was not able to demonstrate the presence of leptines in all of the low TGA resistant clones. Whereas leptines have been found only in *S. chacoense,* other wild *Solanum* species such as *S. demissum, S. polyadenium,* and *S. jamesii* are reported to be as resistant to the CPB as *S. chacoense* (17). These latter 3 species have either dem, tom, or a mixture of both in their leaves (10). Thus, the relationship between quality or type of glycoalkaloid in leaves of potato plants with their resistance to CPB is not clear.

Until recently, leaves of *S. chacoense* were believed to contain only the leptines, leptinines, and sol and chac, while resistant *S. commersonii* was reported to contain only sol and chac (10). Osman et al. (6) found accessions of *S. chacoense* and an accession of *S. commersonii* that contained no sol or chac, but instead had major amounts of a mixture of two other glycoalkaloids, dem, and a new glycoalkaloid, commersonine (com). Apparently, *S. chacoense* and *S. commersonii* are polymorphic for the types of glycoalkaloids contained in individual collections of the two species. According to Torka (17), *S. chacoense* is also polymorphic for

CPB resistance, and *S. commersonii* is probably polymorphic. Earlier methods of glycoalkaloid analysis may have failed to detect the presence of com in resistant wild species and hybrids. The potency of com in repelling the CPB is not known, but this new glycoalkaloid could be important in the resistance mechanism of *S. chacoense*.

McCollum and Sinden (5) selected clones of *S. chacoense* that differed qualitatively in the glycoalkaloids they produced in their tubers. One clone (PI 275138.6) synthesized only com and a trace of dem, with no sol or chac. Another clone (PI 133656) synthesized only sol and chac. The F_1 progeny from crosses of these two clones synthesized major amounts of com, sol, and chac. Certain F_2 clones synthesized new glycoalkaloids formed by recombinations of the aglycone from one parent with one or more sugar moieties from the other parent. In the present investigation, we exposed selected F_2 clones producing different types of glycoalkaloids to a field infestation with CPB to determine whether the type of glycoalkaloid found in leaves of *S. chacoense* influenced resistance to CPB. We also analyzed leaf samples for TGA contents to determine the effect of concentration.

Materials and Methods

Resistance Test

Tubers of 20 selected *S. chacoense* Bitter F_2 clones, seed pieces of *S. tuberosum* L. 'Katahdin,' and tubers of a hybrid clone *S. tuberosum* 'Katahdin'×*S. demissum* Lindl. PI 160221 were planted in peat pots in the greenhouse. After 3 weeks of growth in the greenhouse, the 10 most uniform plants of each clone were transplanted to the field on 5/23/78. Plants were completely randomized in a 20 hill×12 row plot (30 cm spacing between plants) surrounded on each side by two guard rows of 'Katahdin'. The plot was protected by applications of carbaryl for the first 4 weeks of growth in the field. The adequacy and uniformity of beetle infestation was assured by collecting adult beetles from another potato plot at Beltsville and placing 10 on each of the plants in the resistance test on 6/28. Resistance factors (number of adults, larvae, and egg masses, and a damage rating) were measured three times, on 7/11, 7/27, and 8/10). For rating damage, the following classes were defined:

0=no damage
1=few leaves eaten (<10% defoliated)
2=many leaves eaten, few stems stripped (ca 10-30% defoliated)
3=many stems stripped (ca 30-60% defoliated)
4=>60% defoliated

Glycoalkaloid Analyses

Leaf samples (ca 5 g) were collected from 2 plants of each of the 20 *S. chacoense* clones at the time final resistance measurements were made on

8/10. 'Katahdin' and the *S. demissum*×'Katahdin' hybrid plants were sampled on 7/27, just before these plants were completely defoliated by the CPB. Leaf samples were weighed and immediately immersed in methanol:chloroform:acetic acid (4:5:1). After Soxhlet extraction with ethanol and concentration of the extract under vacuum (14), aliquots (equivalent to 1 g leaf tissue) of the aqueous extract were analyzed for types of glycoalkaloids present (5) and TGA contents. For qualitative analyses, aliquots equivalent to 5 mg and 20 mg of each aqueous extract were applied to thin-layer chromotography (TLC) plates (Silica gel 60, EM Laboratories, Inc.[3]) Authentic glycoalkaloids (com, dem, sol, chac) were cochromatographed with aliquots of the foliar extracts to identify these four glycoalkaloids in the leaf extracts. The TLC plates were developed with chloroform:methanol:1% ammonium hydroxide (200:180:100). Glycoalkaloids were visualized with iodine. Ammonia precipitates of extracts that contained leptine-type glycoalkaloids, as determined from gas-liquid chromatography (GLC) analysis of aglycone mixtures, were also analyzed by TLC with ethyl-acetate:pyridine:water (5:2:1) as the developing solvent (4, 11).

Samples equivalent to 0.5 g fresh wt of the aqueous extracts were filtered, extracted with chloroform, and concentrated to dryness under an airstream. The extracts were hydrolyzed under reflux with 1 ml of methanol: conc HCl (8:1) for 4 hours, as described by Kuhn and Löw (4). Aglycones were extracted from hydrolysates into chloroform by adding 2 ml of conc ammonium hydroxide and 2 ml of chloroform. The chloroform layer was removed and the aqueous phase was extracted 2 more times with chloroform. Combined chloroform extracts were washed 2× with an equal volume of water and the chloroform evaporated under an air stream. The chloroform extracts were analyzed by GLC for aglycone composition and then titrated (2) to determine TGA concentration. Samples of the ammonia precipitated plant extracts were also hydrolyzed with 2 N H_2SO_4 to determine the ratio of demissidine:solanidine (7), and the ratio of saturated:unsaturated leptinidine-type aglycones. Tomatine (Sigma Chemical Corp.)[3] was used as a quantitative standard for the titrations, and adjustments were made for the differences in molecular weights of the various glycoalkaloids.

For GLC analysis of the aglycone(s), the method of Osman and Sinden (7) was used with the following minor modifications: A Varian Model 3700 fitted with a 0.9-m×0.6-cm glass column packed with 1% SE-30 on Gas Chrom. Q (100/120 mesh) was used with a flow rate of 30 ml of He/min. Temperature programming of 6°C/min from 190°C to 255°C was used to separate the aglycones. For confirmation of the TLC and GLC identifications of leptine-type glycoalkaloids in foliage of certain of the F_2 clones, individual glycoalkaloids were isolated by preparative TLC. The isolated glycoalkaloids were hydrolyzed and the sugars present in the

hydrolysates were identified by GLC (6). Aglycones in hydrolysates of isolated glycoalkaloids were identified by GLC-mass spectral analysis.

Results and Discussions

Resistance

On 7/11/78 only 20 adults and 280 egg masses were found in the entire plot, and clones did not differ significantly in number of adults or egg masses. However, clones did differ significantly ($p=0.01$) in average damage ratings and numbers of larvae per plant on this date. 'Katahdin' had an average damage rating of 2.3, with 15.0 larvae per plant, while the most susceptible *S. chacoense* clone (clone #20, [Table 1]) had a damage rating of 1.5, and only 5.1 larvae per plant. The 'Katahdin'×*S. demissum* hybrid clone had an average damage rating of 2.3, with 14.2 larvae per plant. The most resistant clone (*S. chacoense* clone #1, [Table 1]) had a damage rating of 0.1, with 1.25 larvae per plant on this date.

Between 7/11 and 7/27 the average damage rating for all 22 clones increased from 0.9 to 1.2; the number of larvae increased from 4.0 to 11.2 per plant; and the number of adults increased from 0.1 to 10.2 per plant. Clones differed significantly in all 3 of these resistance measurements. Between 7/11 and 7/27 the average number of egg masses decreased from 1.4 to 0.8 per plant, with no significant differences among clones on either of the dates. Eight of the 10 'Katahdin'×*S. demissum* hybrid plants and 7 of the 10 'Katahdin' plants in the plot were completely defoliated.

Since we were primarily interested in differences in resistance among the *S. chacoense* clones that synthesized different types of glycoalkaloids, we waited until half of the plants of the most susceptible *S. chacoense* clone (clone #20) were defoliated before taking the final measurements on 8/10 (Table 1).

Glycoalkaloids

The composition of the glycoalkaloid mixtures found in leaves on 8/10 was similar to, or identical with, the composition previously found in tubers for most of the 20 clones (5). However, no leptine-type glycoalkaloids were detected by GLC of hydrolysates and TLC of ammonia precipitates in tubers of the 3 clones that had major amounts of these unusual glycoalkaloids in their leaves (clones 2, 6, and 15 [Table 1]). Kuhn and Löw (4) reported that tubers of the *S. chacoense* plants they analyzed also did not contain leptine-type glycoalkaloids.

Of the 17 F_2 clones that lacked leptines, 9 had com, dehydrocom, or mixtures of both, as their major foliar glycoalkaloids; and 8 had sol (with or without chac), dihydrosolanine (dihydrosol) + dihydrochaconine (dihydrochac), or mixtures of all four of these glycoalkaloids (Table 1). Com and dehydrocommersonine (dehydrocom) both have commetetraose as the sugar moiety of the glycoalkaloid (Fig. 1). They differ only in the aglycone,

TABLE 1. *Damage rating, number of Colorado potato beetle larvae and adults, and foliar TGA content of 20 f_2* Solanum chacoense *clones, August 10, 1978.*

Clone[1]	Foliage damage (rating)[2]	Larvae per plant	Adults per plant	Foliar TGA (mg/100 g fresh wt.)	Major glycoalkaloid
1	0.5	4.4	5.3	307	commersonine
2	0.7	8.2	6.8	473	leptines[3]+dihydrosolanine +dihydrochaconine
3	0.8	3.1	4.5	225	commersonine[5]
4	0.8	10.5	5.0	496	dehydrocommersonine
5	0.9	6.8	9.0	382	dehydrocommersonine
6	1.1	9.2	3.3	468	leptines[6]+commersonine
7	1.1	3.7	6.8	339	dehydrocommersonine
8	1.3	6.8	14.5	396	commersonine
9	1.4	8.1	11.1	121	dehydrocommersonine
10	1.5	14.7	12.3	342	solanine+chaconine
11	1.6	12.4	9.6	525	dihydrosolanine+dihydrochaconine[4]
12	1.8	11.1	13.7	544	dihydrosolanine+dihydrochaconine[4]
13	2.1	9.1	15.5	152	solanine+chaconine
14	2.3	8.8	12.9	250	dehydrocommersonine
15	2.3	10.2	8.3	160	leptines[3]+dihydrosolanine +dihydrochaconine[4]
16	2.3	27.2	17.4	301	solanine
17	2.8	8.9	12.1	196	dehydrocommersonine
18	2.8	10.5	12.0	348	solanine+chaconine
19	3.1	21.5	27.8	62	solanine+chaconine
20	3.5	15.7	14.8	43	dihydrosolanine+dihydrochaconine[4]
Mean[7]±S.E.	1.7±0.3	10.5±4.2		11.1±3.3	307±36

[1]Clones ranked by damage ratings.
[2]0=no damage, 4=defoliated. See Materials and Methods for complete rating scale.
[3]Mixture of leptine-type glycoalkaloids with solatriose and chacotriose sugar moieties (4, 15). Aglycone analyses showed the following aglycone composition in percentages of total: acetyl-leptinidine (ca 10%), leptinidine (ca 10%), acetyl-dihydroleptinidine (ca 20%), dihydroleptinidine (ca 20%), demissidine (ca 30%), and solanidine (ca 10%).
[4]Solanine+chaconine (10-30%) (solanidine aglycone) also detected.
[5]About 20% dehydrocommersonine (solanidine aglycone) also detected.
[6]Mixture of leptine-type glycoalkaloids with commetetraose sugar moiety. Aglycone analyses showed the following aglycone composition, in percentages of total: acetyl-dihydroleptinidine (ca 30%), dihydroleptinidine (ca 30%), and demissidine (ca 40%).
[7]Mean of 10 plants of each clone.

which is saturated (demissidine) in com and unsaturated (solanidine) in dehydrocom. Sol and dihydrosol, and chac and dihydrochac, also differ from each other only in the saturation of the aglycone. The other three clones (clones 2, 6, and 15 [Table 1]) have complex mixtures of glycoal-

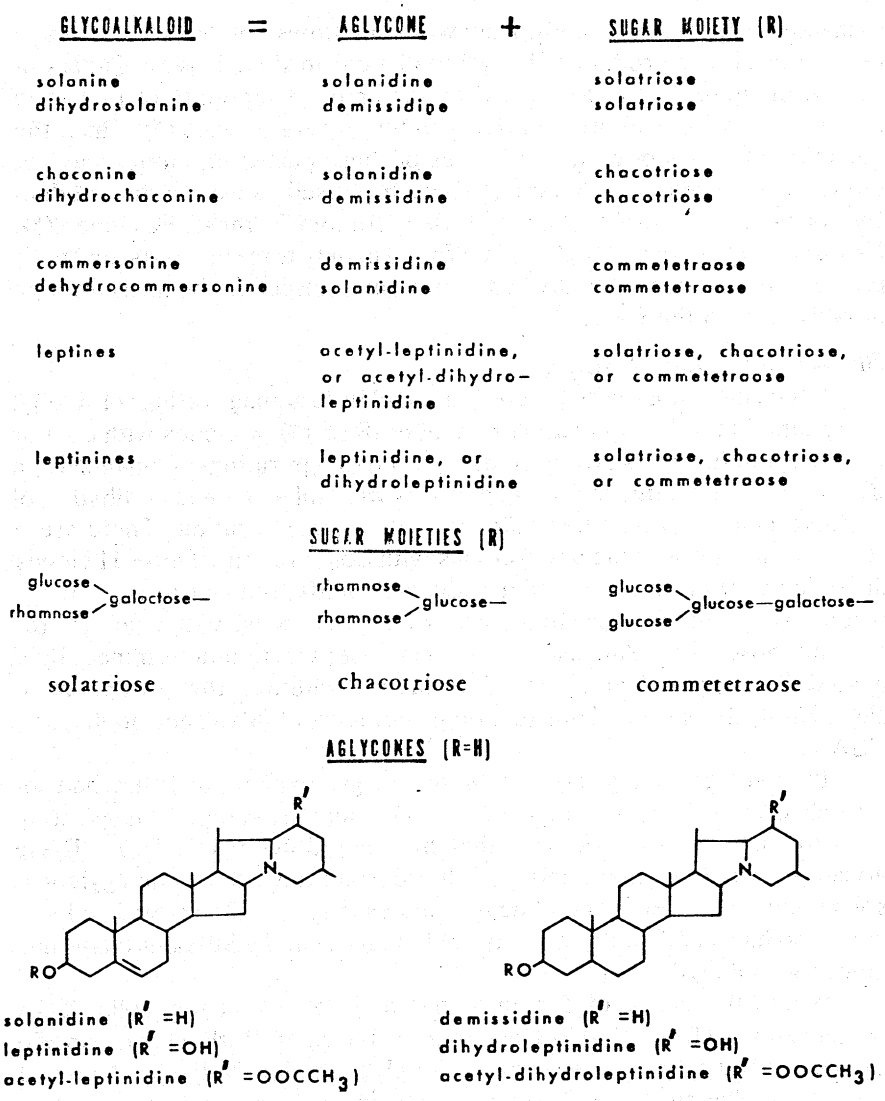

FIG. 1. Types of glycoalkaloids in foliage of F_2 *Solanum chacoense* clones.

kaloids that have these same three sugar moieties, but in addition to the solanidine and demissidine aglycone moieties, they also have leptinidine, 23-acetyl-leptinidine, dihydroleptinidine, and 23-acetyl-dihydroleptinidine as aglycones.

While traces of other glycoalkaloids were not detected in either tuber (5) or leaf extracts of most of the F_2 clones with sol and chac, many clones with com or dehydrocom as their major glycoalkaloid contained traces of glycoalkaloids that were chromatographically indistinguishable from dem,

β-chaconine (β-chac), or both. Dem was sometimes not detected in tubers (5) of clones that produced this glycoalkaloid in their leaves. Tubers of certain of these 20 F_2 clones had minor or trace amounts of β-chac in combination with dehydrocom but without any sol or chac (5). Thus, the detection of traces of β-chac in leaves of these particular clones was not unexpected. A tentative hypothesis was proposed to explain the production of β-chac in combination with dehydrocom in these F_2 clones (5). However, both dem and β-chac were found in only trace amounts, and their presence or absence probably had only a minor effect on the measurement of resistance to the CPB.

Glycoalkaloids and Resistance

If the clones are ranked according to relative damage ratings (Table 1), it appears that a disproportionate number (8 of 11) of clones with com or dehydrocom have lower than mean (1.7) damage ratings. Conversely, a disproportionate number (7 of 9) of clones with sol +/− chac or dihydrosol + dihydrochac have higher than the mean damage rating. There are 5 clones with sol +/− chac and 6 clones with dehydrocom. These 11 clones differ in the sugar moieties of the glycoalkaloids, but not in type of aglycone. We grouped these clones into two classes: those with commetetraose and those with solatriose +/− chacotriose; we then determined, by a nested, hierarchical analysis of variance, whether the groups were significantly different in damage ratings, numbers of larvae and adults, and TGA contents.

The average damage rating (2.4) for the group of 5 clones that had sol +/− chac was significantly higher ($p=0.05$) than the average damage rating (1.5) for the group of 6 clones that had dehydrocom (Table 2). These glycoalkaloids (sol, chac, and dehydrocom) all have the same agylcone, solanidine, but differ in their sugar moieties (Fig. 1). Clones with sol+/− chac also had significantly more ($p=0.01$) larvae and adults per plant than clones with dehydrocom.

Within the group of 5 clones that had sol +/− chac, foliar TGA contents ranged from 62 to 348 mg/100 g fresh weight. Within the group of 6 clones that had dehydrocom as the major glycoalkaloid, foliar TGA ranged from 121 to 496 mg/100 g. The differences in resistance between the two groups of clones were probably not caused by differences in TGA levels since the average TGA levels were about the same for both groups and were not significantly different.

Comparisons of the resistance measurements for the 3 clones that had mixtures of dihydrosol (solatriose − demissidine) and dihydrochac (chacotriose − demissidine) with the resistance measurements for the 3 clones that had com (commetetraose − demissidine) also showed highly significant effects of the sugar moiety of the major glycoalkaloids on all 3 resistance measurements. While the type of sugar moiety of the glycoalkaloids appeared to influence the effect of the glycoalkaloid on the CPB,

TABLE 2. — *Effect of differences in the sugars and aglycones of foliar glycoalkaloids on resistance to the Colorado potato beetle in 20 F_2* Solanum chacoense *clones.*

No. of clones	Foliage damage (rating)[1,2]	Larvae per plant[1]	Adults per plant[1]	Major glycoalkaloids[3] Sugar moieties	Aglycones	Foliar TGA[1] (mg/100 g fresh wt.)
	commetetraose vs. solatriose +/− chacotriose, solanidine aglycone					
5	2.4 a	16.1 a	13.2 a	solanine+/−chaconine[4]	solanidine	241 a
6	1.5 b	7.8 a	9.5 b	commersonine	solanidine	297 a
	commetetraose vs. solatriose+chacotriose, demissidine[5] aglycone					
3	2.3 a	13.1 a	12.7 a	solanine+chaconine	demissidine	371 a
3	0.8 b	4.8 b	8.1 b	commersonine	demissidine	309 a
	solanidine vs. demissidine,[5] solatriose+chacotriose sugars					
5	2.4 a	16.1 a	13.2 a	solanine+/−chaconine[4]	solanidine	241 a
3	2.3 a	13.1 a	12.7 a	solanine+chaconine	demissidine	371 a
	solanidine vs. demissidine,[5] commetetraose sugar					
6	1.5 a	7.8 a	9.5 a	commersonine	solanidine	297 a
3	0.8 a	4.8 a	8.1 a	commersonine	demissidine	309 a
	demissidine[5] vs. leptinidine,[6] solatriose+chacotriose sugars					
3	2.3 a	13.1 b	12.7 b	solanine+chaconine	demissidine	371 a
2	1.5 a	9.2 a	7.6 a	solanine+chaconine	demissidine+ leptinidines	317 a

[1]Within each column (glycoalkaloid comparisons), means followed by different letters are significantly different at the 5% level of probability, as determined by an F test.
[2]Rating system: 0=no damage, 4=defoliation. See Materials and Methods for complete rating system.
[3]See Fig. 1 for sugar and aglycone structures.
[4]One of these 5 clones had only solatriose.
[5]Some clones with demissidine aglycone also had solanidine, in various ratios of demissidine:solanidine (95:5 to 5:1).
[6]The two clones (clones 2 and 5, Table 1) with leptinidine-type aglycones had a mixture of aglycones in hydrolysates of the foliar extracts (see Table 1).

the type of aglycone (solanidine vs. demissidine) did not. Resistance measurements of the 4 clones that had solatriose + chacotriose as the sugar moieties and solanidine as the aglycone of their leaf glycoalkaloids did not differ significantly from those of the 3 clones with the same sugar moieties, but with demissidine or mixtures of demissidine and solanidine as the aglycone. Likewise, clones having commetetraose but differing in type of aglycone (solanidine vs. demissidine) did not differ significantly in resistance.

Leptines are reported to be the resistance factors for CPB in *S. chacoense* (15). Our results indicate that, while leptines may contribute to resistance, this type of glycoalkaloid is not essential for the expression of resistance in *S. chacoense* plants. Leptines were identified in leaves of 3 of the 20 F_2 clones. Two of these clones had glycoalkaloids with solatriose and chacotriose sugar moieties and mixtures of aglycones that included acetyl-leptinidine (4, 15), the aglycone of leptine I (Table 1). When the resistance measurements for these two clones were compared with those of the 3 clones that had the same sugar moieties and a similar ratio of saturated:unsaturated aglycones, but without leptinidine aglycones, the two clones with leptine glycoalkaloids were more resistant (Table 2). However, only the differences in average numbers of larvae and adults per plant were significant.

Clone 1, with the lowest average damage rating (0.5) and only 4 larvae and 5 adults per plant (Table 1), contained no leptines. This clone had only com, at a moderate TGA concentration of 307 mg/100 g fresh wt. The clone that had ca 30% of the TGA in the form of a leptine glycoalkaloid with a commetetraose sugar moiety (clone 6, [Table 1]) also had a higher foliar TGA concentration (468 mg/100 g) than clone 1, yet was more susceptible to CPB than clone 1 with an average damage rating of 1.1 and with 9.2 larvae and 3.3 adults per plant. Thus, our results indicate that *S. chacoense* plants can be highly resistant without the presence of leptines in their leaves.

Schreiber (10) speculated that the xylose sugar and the saturation of the aglycone in dem were responsible for the greater activity of dem, compared with either sol or chac, in deterring the CPB from feeding. Sol and chac, which differ in the composition of their sugar moieties (Fig. 1), are almost equal in activity toward the CPB (15). Our results indicate that both com and dehydrocom are more active than sol, or mixtures of sol and chac; dehydrocom differs from sol and chac only in the size and composition of the sugar moiety (Fig. 1). Com and dehydrocom do not contain xylose, and dehydrocom appeared to be as active as com in limiting damage and numbers of adults and larvae. Therefore, our results indicate that the number of sugar residues (tetrasaccharide vs. trisaccharide) in the sugar moiety may be as important as the presence or absence of a particular sugar such as xylose. Our results also suggest the possibility that the saturation of

the aglycone may not be important in determining the relative activity of a potato glycoalkaloid towards the CPB. Tests with pure glycoalkaloids infiltrated into leaf disks, or incorporated into artificial diets, are needed to define the effects of the different chemical structures of the recently identified potato glycoalkaloids (6, 7, 13) on feeding activity of the CPB.

TGA Concentrations and Resistance

In making the comparisons among clones that differed in types of glycoalkaloids in their leaves, the clones were classified according to the chemical nature of the glycoalkaloids without regard to levels of TGA. Reports in the literature suggest that high TGA concentrations in solanaceous plants may be important in deterring CPB and leafhopper feeding (9, 14, 16). Although there were highly significant differences in foliar TGA levels of individual clones, the differences in average TGA levels between groups of clones with a common type of glycoalkaloid were not significant (Table 2). Therefore, it appears that the differences we observed in resistance between groups of clones with different types of glycoalkaloids were not caused by differences in TGA concentrations.

For all the *S. chacoense* clones, disregarding the different types of glycoalkaloids found in the leaves, the correlation coefficient for the relationship of damage rating to log of TGA concentration was highly significant ($r=-0.67$, $p=0.01$) (Fig. 2). However, the coefficients of correlation between log of foliar TGA and number of larvae and between log of foliar TGA and number of adults were low and not significant ($r=-0.19$, N.S., and $r=-0.22$ N.S., respectively). Thus the level of foliar TGA did appear to influence the damage to the *S. chacoense* plants, but did not significantly affect the numbers of adults or larvae. Perhaps higher TGA levels act as a feeding deterrent for larvae and adults, thus reducing damage; but do not act as a repellent. Measurements of total larval weights per plant, instead of total numbers, might help to clarify the relationship between TGA levels and resistance.

Commercial potatoes generally have foliar TGA levels of less than 100 mg/100 g fresh wt (1) and, with the exception of Kennebec, have only sol and chac as their major foliar glycoalkaloids (13). If TGA content is a factor in the resistance of potatoes to CPB, then commercial cultivars might be expected to be damaged as much as clones 19 and 20 of *S. chacoense* were; these 2 clones had only sol and chac at concentrations of 63 and 43 mg/100 g, respectively (Table 1). 'Katahdin' and a 'Katahdin'×*S. demissum* hybrid clone with foliar TGA concentrations of 42 and 30 mg/100 g, on 7/27, respectively, were completely defoliated by 8/10, whereas clones 19 and 20 of *S. chacoense* were only partially defoliated on this date. Thus, some of the *S. chacoense* plants with low TGA may have resistance factors other than the glycoalkaloids we detected.

In breeding potatoes for resistance to the CPB, it may be necessary to evaluate both TGA levels and composition. While other types of glycoal-

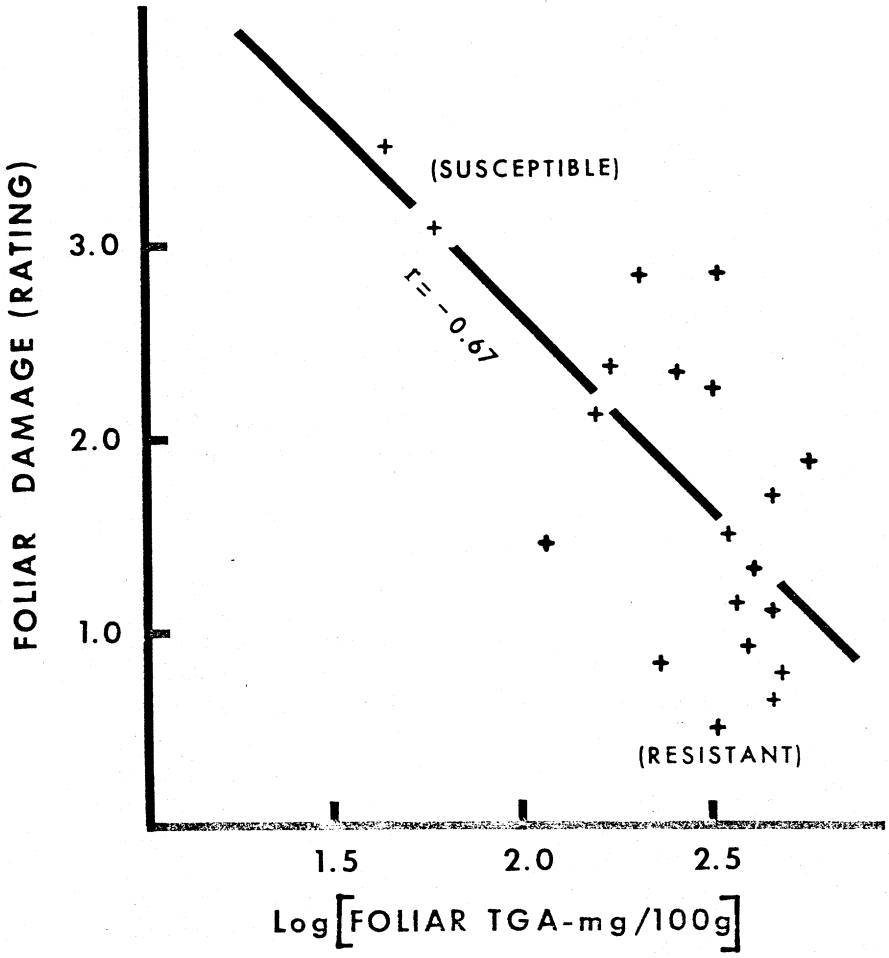

FIG. 2. Relationship between foliar damage and levels of total glycoalkaloids (TGA) in foliage of 20 F_2 *Solanum chacoense* clones.

kaloids, such as com and dem, may be no more toxic to animals than sol and chac, there is no history of safe consumption of com, dem, or the leptines. Sol and chac are normal constituents of all commercial potato tubers and only if levels in tubers exceed 20 mg/100 g fresh weight is consumption considered even potentially hazardous (12). However, tuber TGA levels tend to be correlated with foliage TGA levels in *S. tuberosum* (1) and hybrid (11) breeding populations. Selection for CPB resistance could result in increased TGA levels in both tubers and foliage. Alternatively, it might be possible to transfer the leptine-type glycoalkaloids from resistant *S. chacoense* clones to *S. chacoense*×*S. tuberosum* hybrids. Since leptines

are found in leaves, and not in tubers (4), some of the hybrids might have resistant foliage and normal tuber glycoalkaloid contents.

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